potentially significant source together with fire and mowing.

The team found that native perennials reduced soil moisture, soil nitrogen, and light to lower levels than did exotic annuals. This ability to outcompete the exotic species for these resources means that native perennials should be able to increase in abundance. This suggests that the current rarity of native perennials at the researchers' site is caused by natives being unable to penetrate the stands of exotic annuals and not by exotic annuals being superior resource competitors.

Annual species tend to allocate fewer resources to roots and more resources to leaf and seed production, a trade-off that should make annuals faster growers and better exploiters of disturbances but weaker competitors for below-ground resources than perennials. The annuals did better under all conditions of disturbance: gophers, fire and mowing.

If a trade-off between competitive ability for California grassland plants is proven, superior competitors would be slow to recover from the disturbance once driven to low densities. At another Californian site, inside a nature reserve, the two dominant native perennial bunchgrasses took 15–20 years to reappear anywhere in a field after it was abandoned to agriculture and a further 25–35 years before they obtain peak abundances, even if fields are surrounded by intact native grasslands, the researchers note.

If exotic annuals were competitively dominant, re-establishment of the native flora would depend on the eradication and continued quarantine of exotics: 'two difficult and costly ventures,' the researchers say.

But if exotic annuals are not superior competitors and dominate because of prior disturbance and the low dispersal abilities, seed production and extreme current rarity of native perennials, 'it may be feasible to restore native California grassland flora to at least parts of its former range,' the team say.

Grass attacks: Native species thriving in an English hay meadow: a new study in California finds rare native grass species may be more effective at competing with exotic grass species than might appear from their current dominance.

Quick guide

Sticklebacks

Catherine L. Peichel[1] and Janette W. Boughman[2]

What is a stickleback? *Gasterosteus aculeatus* is a small teleost fish, abundant in marine and coastal freshwater habitats throughout the Northern hemisphere. Freshwater populations have evolved a remarkable diversity of morphologies, behaviors and life histories since the end of the last Ice Age, 10,000 years ago, when marine sticklebacks invaded newly created freshwater lakes and streams. This diversity is so great that sticklebacks were originally classified as over 100 separate species!

Why do sticklebacks appear on the Dutch guilder? Sticklebacks have distinct and well-studied reproductive behaviors. One of the founding fathers of the study of ethology was Niko Tinbergen, a Dutchman. Much of Tinbergen's work focused on determining the key signals that elicit behavioral responses during the elaborate courtship ritual of male and female sticklebacks. His work spawned a large school of behaviorists who have worked on sticklebacks. The result is that more is known about reproductive behavior and biology in sticklebacks than in almost any other system. Tinbergen was awarded the 1973 Nobel Prize for his pioneering work, hence the appearance of the stickleback on the (now-defunct) Dutch guilder.

What have sticklebacks done for us lately? Stickleback research is alive and swimming! Sticklebacks are still widely used in behavioral studies, including studies on cognitive processes such as spatial learning and social learning, and personality traits such as levels of aggression and risk taking. Stickleback research has given us some of the best empirical tests of important theories of sexual selection and signal evolution. And stickleback research is central to developing new directions that integrate ecological processes and life history theory with sexual selection. Work using sticklebacks is increasingly going beyond behavior, encompassing and integrating the fields of evolution, ecology, physiology, toxicology, parasitology and molecular genetics. Research on sticklebacks is as diverse as the fish themselves and we shall highlight just a few of the areas where sticklebacks are making a big splash.

A male stickleback courting a less-than impressed female.

What can sticklebacks tell us about how new species form? Throughout the range of sticklebacks, there are many instances where divergent forms come into contact with each other, yet are reproductively isolated. The isolating mechanisms between these divergent populations are things like differences in male morphology and behavior and female preference for these traits, and ecological selection against hybrids. Although reproductive isolation is nearly complete in the wild, virtually any of these forms can be crossed with each other in the laboratory to generate viable and fertile offspring which can be used in genetic, ecological and behavioral studies. Sticklebacks thus provide an excellent system to experimentally address questions such as: What are the ecological forces that drive the formation of new species? What are the roles of sexual and natural selection in driving reproductive isolation? What are the genetic and molecular mechanisms that underlie traits contributing to reproductive isolation? Current work is addressing these questions and should lead to a more complete picture of the ecological, evolutionary and genetic processes that lead to speciation.

What can sticklebacks tell us about ourselves? These little fish have a lot to teach us about our own behavior and evolution. Watching a male stickleback trying to get a female stickleback into his nest is pretty much like watching a scene in a bar on a Saturday night! In addition to their behavior, the fish differ in many other traits directly relevant to human disease, including longevity, disease susceptibility and response to environmental contaminants. One direct example involves host–parasite interactions in sticklebacks. Sticklebacks are exposed to a wide variety of parasites in the wild, and there is natural variation in susceptibility to infections among individuals and populations, just as in humans. The fish also respond to environmental pollutants such as estrogens and androgens and occur naturally in many of the freshwater streams and lakes threatened by pollution in the Northern Hemisphere. This makes them ideal sentinel organisms for the detection of environmental contaminants. Interestingly, adaptation of sticklebacks to different freshwater environments has occurred in roughly 10,000 generations — similar to the number of generations in which modern humans have colonized different environments around the world. Human and stickleback populations may thus show similar diversity and genetic architecture of many complex traits.

Is there a stickleback genome project? Not yet! The recent development of a genetic linkage map for sticklebacks has made it possible to map the number and location of chromosome regions that control many of the interesting traits that vary in stickleback populations. A major goal of current research is to use these genetic map positions to identify the genes and molecular changes that underlie the appearance of new morphological, behavioral and physiological traits in vertebrates. Many of the tools required for these studies, such as BAC and cDNA libraries, transgenic technologies and a genome-wide physical map are currently being developed at the Stanford Genome Evolution Center. Given the rich history of previous studies, and the large number of traits that can be studied in sticklebacks, we hope that the well-integrated genetic and physical maps of this new model organism will soon be complemented by a full-scale genome sequencing project.

Where can I find out more about sticklebacks?

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[1]Division of Human Biology, Fred Hutchinson Cancer Research Center, 1100 Fairview Ave North, PO Box 19024, Seattle, Washington 98109-1024, USA. [2] Department of Zoology, University of Wisconsin-Madison, Madison, Wisconsin 53706, USA.